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DIFFERENCES IN DIET AND CHICK PROVISIONING BETWEEN ADULT ROSEATE AND SANDWICH TERNS IN PUERTO RICO[1]

DAVID A. SHEALER
Department of Biology, Colgate University, Hamilton, NY 13346,
e-mail: dshealer@center.colgate.edu

Abstract. I analyzed regurgitations from adult Roseate Terns (*Sterna dougallii*) and Sandwich Terns (*S. sandvicensis*) breeding in southwestern Puerto Rico in 1992 and 1993, and compared them with observations of prey delivered to chicks from 1991 to 1993 to determine similarities in the prey base for the two tern species during different stages in the breeding cycle, and differences between the diets of adults and chicks. I sampled prey fish at Turrumote lagoon where terns regularly fished to determine if the species composition of the fishes in the lagoon was representative of the prey base taken by terns. Adult Roseate Terns fed primarily on dwarf herrings (*Jenkinsia lamprotaenia*) and anchovies (*Anchoa* spp.), and fed chicks mostly dwarf herrings and sardines (*Harengula* and *Opisthonema* spp.); few anchovies were fed to chicks. Adult Sandwich Terns fed primarily on silversides (*Hypoatherina harringtonensis*) and sardines, and fed chicks mostly sardines and dwarf herrings; few silversides were fed to chicks. In 1992, both tern species apparently compensated for a lack of sardines by feeding their chicks proportionally more dwarf herrings. Diet diversity was greater for Sandwich than for Roseate Terns both in regurgitations and in prey delivered to chicks. Dietary overlap between the two species was low prior to, but converged following, chick hatching. Both species fed chicks increasingly larger prey as the chicks grew larger, but patterns were not consistent among years. Prey samples taken from Turrumote lagoon were representative of, but not in proportion to, the species of prey fed to chicks. These results indicate that although both Roseate and Sandwich Terns in Puerto Rico fed primarily on the same few species of fish, they did so in different proportions. This finding is consistent with an earlier study demonstrating foraging habitat segregation in these two species.

Key words: chick-provisioning, diet, prey selection, Roseate Tern, Sandwich Tern, Sterna.

INTRODUCTION

Diet and food-provisioning studies of seabirds commonly are conducted at breeding colonies where adults return to feed mates or chicks. The information obtained from these studies can be useful in helping to elucidate such factors as foraging-trip duration (Hulsman and Smith 1988), temporal changes in prey capture (Safina et al. 1990), intercolony variability in diet (Frank 1992), energetic considerations (Massias and Becker 1990), and effects on breeding performance (Vermeer 1980, Monaghan et al. 1989a). Multi-year studies of seabird diets may help to determine yearly distribution of, and variation in, prey stocks in localized areas around breeding colonies (Monaghan et al. 1989b, Berruti et al. 1993, Bertram and Kaiser 1993). Because seabirds and fish stocks are inextricably linked, the breeding performance of seabirds can be used to gauge the health of the marine ecosystem surrounding breeding colonies (Monaghan et al. 1989b, Furness and Nettleship 1991). Reproductive failure of entire seabird colonies over a period of years can be an indication that local fish stocks have either declined drastically or crashed (Monaghan et al. 1992).

To date, most studies of seabird diets have been conducted in temperate latitudes, where strong seasonal bursts of primary productivity support thousands, or even millions, of breeding individuals. Little is known about annual or seasonal variation in diet of many tropical seabird species. Relative to temperate latitudes, primary productivity in many tropical marine ecosystems is low and seasonally invariable (Raymont 1980). As a result, many species of tropical seabirds adopt a more pelagic habit, feeding at great distances from the breeding colony. Previous diet studies of tropical seabirds mostly have involved these pelagic species, and most studies, although quantitative (Brown 1975, Schreiber and Hensley 1976, Diamond 1983), did not assess temporal differences in diet (but see Harrison et al. 1983).

I studied the adult diets and chick provision-

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ing of Roseate Terns (*Sterna dougallii*) and Sandwich Terns (*S. sandvicensis*) in southwestern Puerto Rico from 1991 to 1993 to determine the prey base for these two species and to examine differences between what adults ate and what they fed to chicks. I undertook this study for two reasons. First, Roseate and Sandwich Terns are classified as inshore species and little is known about the feeding ecology of these terns in tropical areas. Second, because terns feed primarily on fishes in the 0- or 1-year class, a multi-year diet analysis can provide insight into annual variation in prey stocks around breeding colonies. Information on the seasonal distribution of these juvenile fishes is of interest because they represent an important link in tropical marine food webs, as they feed on zooplankton (Powles 1977) and are eaten by larger predatory fish, some of which are commercially important as game fish (Erdman 1967, Roger 1994).

Roseate and Sandwich Terns in Puerto Rico partition foraging habitat (Shealer 1996): Roseate Terns feed primarily in deep, open water, and they rely heavily on predatory fish to drive prey fish to the surface; Sandwich Terns feed less frequently over predatory fish and are more often found singly or in small flocks in inshore areas. I expected that these differences in foraging habitat would be reflected in differences in the prey base of these two species. During the chick-rearing period, however, both species commonly foraged together at a tidal lagoon at Cayo Turrumote, near the breeding colonies (Shealer and Burger 1995, Shealer 1996), and I sampled prey fish there to determine if the species composition was representative of the prey base adult terns fed to chicks.

METHODS

STUDY AREA

This study was conducted from May to July, 1991–1993, on three offshore coral cays located along the southwestern coast of Puerto Rico (17°56′N, 67°05′W), near the village of Parguera. In each year, Roseate and Sandwich Terns nested on two cays approximately 2–4 km south of the mainland, but they did not use the same cays in successive years. All cays used for nesting were similar in that they were flat coral rubble islands along the outer reef zone (see Shealer 1996, for a map of the study area).

ADULT DIETS

I monitored the arrival and egg-laying patterns of terns in the spring. Approximately one week before chicks began to hatch, I erected a blind in a location that enabled me to see several nests of each species. As part of an ancillary study, adult Roseate and Sandwich Terns were trapped on nests by placing a wire mesh treadle trap over the eggs. Trapping dates were between 22 May and 18 June, 1992, and 28 May and 15 June, 1993. Only adults that had been incubating for at least two full weeks were trapped to minimize the potential for nest desertion. Roseate Terns were banded with metal U.S. Fish and Wildlife Service bands and one to three plastic colorbands; Sandwich Terns were not banded, but some were colormarked with nontoxic magic marker to facilitate identification. In 1993 I collected any food boluses regurgitated by adult terns during handling. Boluses were stored temporarily in ethanol for transport back to the laboratory, where they were weighed, sorted, and contents identified to lowest taxon, using Dekhnik et al. (1966), Powles (1977), and Robins and Ray (1986) as references. Laboratory analysis was not conducted on boluses in 1992; instead I took qualitative field notes on bolus contents.

CHICK PROVISIONING

In each year, the first chicks began to hatch during the first week of June, and hatching peaked approximately one week later. I banded newly-hatched Roseate Tern chicks with U.S. Fish and Wildlife Service bands and plastic colorbands to identify individuals at a distance. Sandwich Tern chicks were not banded but were marked with a nontoxic magic marker to distinguish study chicks from others. In each year I selected 10 nests of each species for studies of chick provisioning. Study nests were selected on the basis of their relative synchrony of hatching (i.e., all chicks hatching within 5 days of one another). The chick-provisioning study began on 13 June (1991), 15 June (1992), and 14 June (1993) to eliminate any potential confounding effects of seasonal variation in prey availability among years. Because Roseate Tern chicks often remained under cover during feeding, I selected nests that hatched only one chick to eliminate confusion about which chick was being fed. Sandwich Terns lay only one egg, so all study chicks were singletons.

For the 3-week period following the hatching of the first study chicks, I conducted daily 2-to 4-hr observations from a blind where I recorded the prey delivered to study chicks of each species. I attempted to identify each prey item to its lowest taxon and noted its length relative to the adult tern's bill. In each year, some prey items were not seen well enough to be identified (< 5% in each year). I therefore categorized them as "unknown" and excluded them from analysis of prey composition but included them in prey-size analyses. Prey sizes were categorized as tiny (< 0.5 x culmen length), small (0.5–1.0 x), medium (1–1.5 x), or large (> 1.5 x).

Most items fed to chicks could be assigned to at least the genus level. However, several species in the family Clupeidae are nearly identical in size and shape and could not be identified to a more specific taxon. Separation to genus and species of these juvenile clupeids is based upon gillraker counts and pigmentation patterns (Ditty et al. 1994), characteristics that are impossible to determine by remote observation. However, these species commonly school together around reefs in the study area (pers. observ.) and elsewhere in tropical waters (Powles 1977). Laboratory analysis of adult boluses revealed three separate species in this group, but for the chick-provisioning study they were all classified as "sardine" (*Opisthonema* or *Harengula*).

PREY SAMPLING

In 1993, I used a monofilament cast net (2.5 m diameter, 6 mm mesh) to sample the prey base at a small, tidal lagoon at Cayo Turrumote. Both Roseate and Sandwich Terns foraged in this lagoon almost daily before and during the breeding season, and frequently were seen carrying fish caught from there toward the nesting colonies to feed chicks. For this reason, I wanted to determine if the species composition of prey fishes in the lagoon was representative of the prey base delivered to chicks. Sampling was conducted on 12 dates from 16 May to 15 July, and consisted of 12 casts within a 30-min period (09:00–09:30), one at each of 12 marked stations around the lagoon. Fish were collected, stored temporarily in ethanol, then transported back to the laboratory where they were sorted, weighed, measured, and identified to species. I snorkeled two underwater transects (25 m each) in the lagoon immediately following net sampling to verify the absence of particular fish species (Shealer 1995).

DATA ANALYSIS

Data from the chick-provisioning study were analyzed by pooling prey deliveries of each tern species into three 1-week periods in each year. These periods roughly coincided with the median ages of the study chicks as a group, determined by daily examinations of chicks. I compared patterns of provisioning among chicks that were 0–1, 1–2, and 2–3 weeks of age. To make the data more categorical, I allowed two days to elapse before collecting data on the next week. The length of the chick period varies among individuals of each species, but for Roseate Terns is 23–27 days, whereas for Sandwich terns it is 27–33 days (Veen 1977, and pers. observ.). After about 20 days of age, the chicks of both species begin to wander toward the water's edge and become difficult to follow. Thus, the feeding study was terminated after the third week in each year.

I tested for differences among prey species delivered by adult terns among weeks in each year and among years using Chi-square tests. I compared daily similarities in the adult and chick diets of the two tern species using Levins' (1968) index of diversity, given as $1/\Sigma p_i^2$, where p_i is the proportion of items in taxon i in the diet. The proportions of items in the diet were then used to compare daily feeding overlap indices from Schoener's (1983) formula, given as $1 - 0.5\Sigma|p_{ih} - p_{jh}|$, where p_{ih} and p_{ij} are the proportions of prey taxon h in the diet of species i and species j, respectively. Individual daily diversity and overlap indices were pooled and then compared using paired-samples t-tests. I chose to pool the data rather than use individual diversities because I was interested in comparing how the two species were partitioning prey on a daily basis. Pooling the data gives the similarity between mean individuals, whereas comparing individual diversities gives the mean similarity and overlap among individuals (Linton et al. 1989). Other statistical tests are identified as they appear. Values presented are means ± SE (unless otherwise indicated); P-values < 0.05 are considered significant.

RESULTS

DIET OF ADULT TERNS

Regurgitations collected from 33 adult Roseate Terns and 22 adult Sandwich Terns during trap-

TABLE 1. Daily species diversity and overlap ($\bar{x} \pm$ SE) of prey regurgitated by adult Roseate and Sandwich Terns and fed to chicks in 1993.

	Adult diet		Chick diet	
	Diversity[a]	Overlap[b]	Diversity	Overlap
Roseate Tern	2.80 ± 0.28	0.16 ± 0.05	3.07 ± 0.16	0.58 ± 0.04
Sandwich Tern	3.19 ± 0.40		4.55 ± 0.34	

[a] Diversity = $1/\Sigma\, p_i^2$ (Levins 1968).
[b] Overlap = $1 - 0.5\,\Sigma\,|p_{ih} - p_{jh}|$ (Schoener 1983).

ping in 1993 revealed 16 fish species from 7 families. Adult Roseate Terns fed primarily on dwarf herrings (*Jenkinsia lamprotaenia*) and anchovies (*Anchoa* sp.), which were numerically most abundant and occurred in almost all daily samples. In 1992, dwarf herrings occurred in 4 of 9 (44.4%) boluses collected, but no anchovies were found. Adult Sandwich Terns in 1993 fed primarily on reef silversides (*Hypoatherina harringtonensis*), a sardine (*Harengula* sp.), and Atlantic thread herrings (*Opisthonema oglinum*). The two boluses collected from Sandwich Terns in 1992 were consistent with those from 1993.

In general, adult Sandwich Terns had a more diverse diet than did Roseate Terns (Table 1). However, on the five days that boluses were collected from both species, the difference in diversity was not significant (paired *t*-test, $t_4 = 0.79$), possibly due in part to the low number of sample days. On a given day, the number of boluses collected was significantly positively correlated with the respective diversity index for Sandwich Terns ($r_5 = 0.78$, $P < 0.05$), but not for Roseate Terns ($r_7 = 0.33$). Although the two tern species fed on only a few species before chicks hatched, they did so in different proportions. As a result, the daily indices of feeding overlap for the two species were low (Table 1).

Mean mass of 14 boluses regurgitated by adult Roseate Terns was 3.38 ± 0.55 g, approximately 3% of body mass (ca. 100 g). Mean mass of 8 boluses regurgitated by adult Sandwich Terns was 8.29 ± 1.71 g, or approximately 4% of body mass (ca. 210 g). Bolus masses of Sandwich Tern regurgitations were significantly greater than those of Roseate Tern regurgitations ($t_{20} = 3.43$, $P < 0.01$). The mean number of items that comprised Roseate Tern boluses was 9.4 ± 1.6 ($n = 19$), and for Sandwich Terns was 4.1 ± 0.7 ($n = 10$), a difference that was significant between the two species (unequal variances $t_{24} = 3.04$, $P < 0.01$). The above data indicate that during a feeding bout, Roseate Terns took many small fish, whereas Sandwich Terns took fewer, larger fish.

CHICK PROVISIONING

From 1991 to 1993 I identified one squid species and 22 species of fish from 17 families delivered by Roseate and Sandwich Terns to their chicks. During the three years of this study, Roseate Terns specialized on only two fish species. The most numerically abundant prey delivered to Roseate Tern chicks were dwarf herrings, which comprised over 53% of all items in all three years. The second most abundant prey delivered by Roseate Terns were sardines. All other species occurred in less than 6% of the prey deliveries by Roseate Terns in any given year.

In all three years, Sandwich Terns delivered a greater diversity of prey species (4.07 ± 0.60) to chicks than did Roseate Terns (2.32 ± 0.40). Although dwarf herrings and sardines comprised the majority of prey deliveries to chicks, a higher proportion of sardines than dwarf herrings was brought to chicks in two of the three years (Fig. 1). Sandwich Terns delivered a higher proportion than Roseate Terns of other fish, such as silversides (*Hypoatherina harringtonensis* and *Atherinomorus stipes*), mackerels (*Scomberomorus* sp.), jacks (*Caranx* spp.), and flyingfish (*Cypselurus* sp.). Sandwich Terns also fed chicks fishes commonly associated with coral reefs, such as damselfish (*Pomacentrus* sp.) and parrotfish (Scaridae), but in small proportion (< 11% in a given year). The pattern of provisioning by Roseate and Sandwich Terns with dwarf herrings and sardines showed a similar trend among years. In 1992, there was a marked increase in the proportion of dwarf herrings, and a concurrent decrease in the proportion of sardines, compared to 1991 and 1993 (Fig. 1).

On a daily basis, Sandwich Terns delivered a higher diversity of prey to chicks than did Roseate Terns in 1993 (paired *t*-test, $t_{14} = 4.58$, $P < 0.001$). The mean daily index of feeding over-

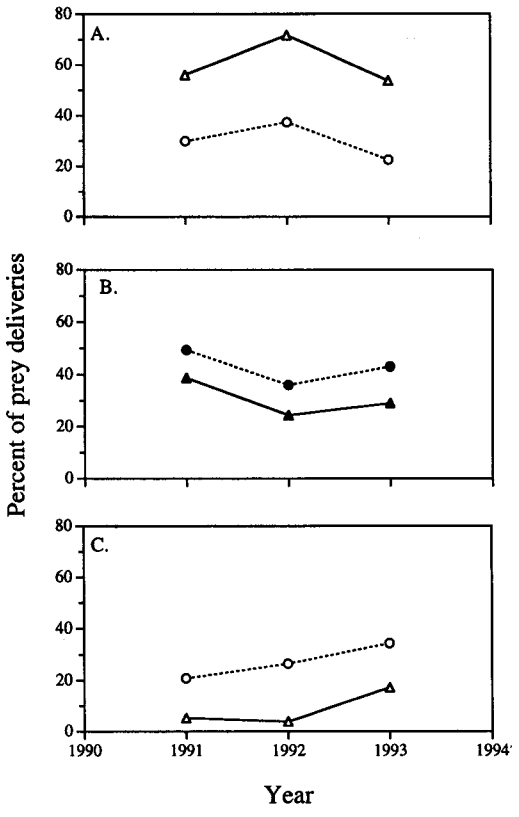

FIGURE 1. Percent of total number of prey deliveries by adults to chicks from 1991 to 1993 that were (A) dwarf herrings, (B) sardines, and (C) other fish. Triangles represent deliveries by Roseate Terns, and circles represent deliveries by Sandwich Terns.

lap between the two tern species during the chick rearing period was considerably greater than during the period prior to hatching (Table 1). The indices of diversity between the two species were not correlated over the 15 days of chick feeding observations ($r_{14} = 0.31$, $P > 0.05$).

The size distribution of prey items delivered by Roseate Terns differed among the 3-week chick period in all years (1991, $\chi^2_6 = 62.1$; 1992, $\chi^2_6 = 96.8$; 1993, $\chi^2_6 = 35.6$; $P < 0.001$ for all tests). In general, prey items delivered to chicks were larger (i.e., longer) as chicks grew older. However, this trend was not consistent among years ($\chi^2_6 = 80.6$, $P < 0.001$). Compared to 1991, Roseate Terns consistently fed chicks smaller fish in 1992 and larger fish in 1993 across the three weeks of the chick period. The size distribution of prey items fed to Sandwich Tern chicks also differed among the 3-week chick period in all years (1991, $\chi^2_6 = 62.8$; 1992, $\chi^2_6 = 65.1$; 1993, $\chi^2_6 = 93.8$, $P < 0.001$ for all tests). The sizes of prey items increased throughout the chick period, but the pattern differed among years ($\chi^2_6 = 82.0$, $P < 0.001$). In general, Sandwich Terns fed chicks smaller fish in 1991 compared to 1992 and 1993.

COMPARISON BETWEEN ADULT AND CHICK DIETS

For both Roseate and Sandwich Terns in 1993, adult diets consisted of different proportions of prey than those fed to chicks (Roseate $\chi^2_5 = 115$, Sandwich $\chi^2_5 = 96.7$, $P < 0.001$ for both tests, Fig. 2). The difference in Roseate Terns was accounted for by the lack of anchovies in the chick diet, but a greater abundance of clupeids, primarily dwarf herrings. For Sandwich Terns, silversides were replaced in the diet of chicks by clupeids as well, but primarily sardines.

PREY SAMPLING

From 16 May to 4 June, 1993, prior to chick hatching, almost all (> 95%) fish caught in Turrumote lagoon were dwarf herrings. No anchovies were caught there before 12 June, despite comprising about 40% of the diet of adult Roseate Terns. Likewise, sardines and anchovies did not enter the lagoon until after 4 June, although they comprised the majority of the diet of adult Sandwich Terns. The absence of sardines and anchovies was verified visually by snorkeling.

A comparison of the two most abundant prey fish species (dwarf herring, sardine) indicated that terns did not deliver them to chicks in the same proportion that I caught them in Turrumote lagoon (Fig. 3). Dwarf herrings were the most abundant fish species in the lagoon until 28 June; they disappeared from the lagoon after that time and were replaced by sardines. However, deliveries of dwarf herrings and sardines to chicks by both tern species remained relatively consistent throughout the chick-rearing period (Fig. 3).

DISCUSSION

The results of this diet study of Roseate and Sandwich Terns in southwestern Puerto Rico indicate that (1) the primary prey base for adults of both species consisted of only two species of fish (dwarf herrings and sardines), and com-

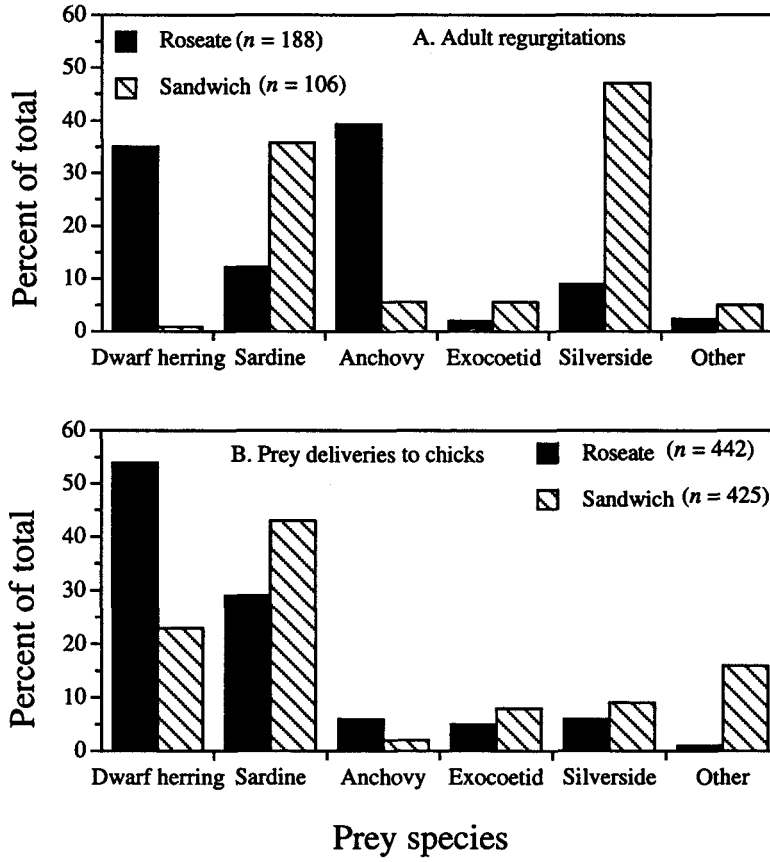

FIGURE 2. Comparison between Roseate and Sandwich Terns of the percentage of prey items (A) identified in adult regurgitations and (B) delivered to chicks in 1993.

prised over 65% of the prey items delivered by each tern species to chicks in all three years of this study, (2) despite this high degree of specialization, the two tern species fed on prey in different proportions, and indices of feeding overlap were low prior to chick hatching, (3) the diets of adult terns consisted of prey items in different proportions than were fed to chicks, and (4) the sizes of prey fed to chicks increased consistently as chicks aged, although there were yearly differences in the magnitude of this trend.

Dwarf herrings and anchovies are common in tropical waters and form large schools in shallow water and around reefs (Powles 1977, Beets and LaPlace 1991). However, anchovies rarely were fed to chicks of either species, suggesting that their availability declined later in the season, or that these fish did not occur close enough to the breeding colony to make traveling for them economical for terns. In Cuba and south Florida, anchovies appear to enter shallow bays and estuaries to spawn in August or September (Dekhnik et al. 1966, Houde and Lovdal 1984), but their inshore abundance at other times of the year is not well known. In 1993, net samples from Turrumote lagoon, where terns commonly foraged, revealed an absence of anchovies prior to 12 June and a low abundance until 20 July (Shealer 1995). Most anchovies regurgitated by adult Roseate Terns were hatching-year juveniles < 30 mm standard length, that presumably were caught in deep, open water over predatory fish schools (Shealer 1995).

A similar dietary shift prior to and after chick hatching was noted for Sandwich Terns in 1993. Silversides (Atherinidae) comprised the majority of bolus contents regurgitated by adults prior to chick hatching. However, Sandwich Terns fed their chicks a very low proportion of silversides in all three years of the provisioning study. Sil-

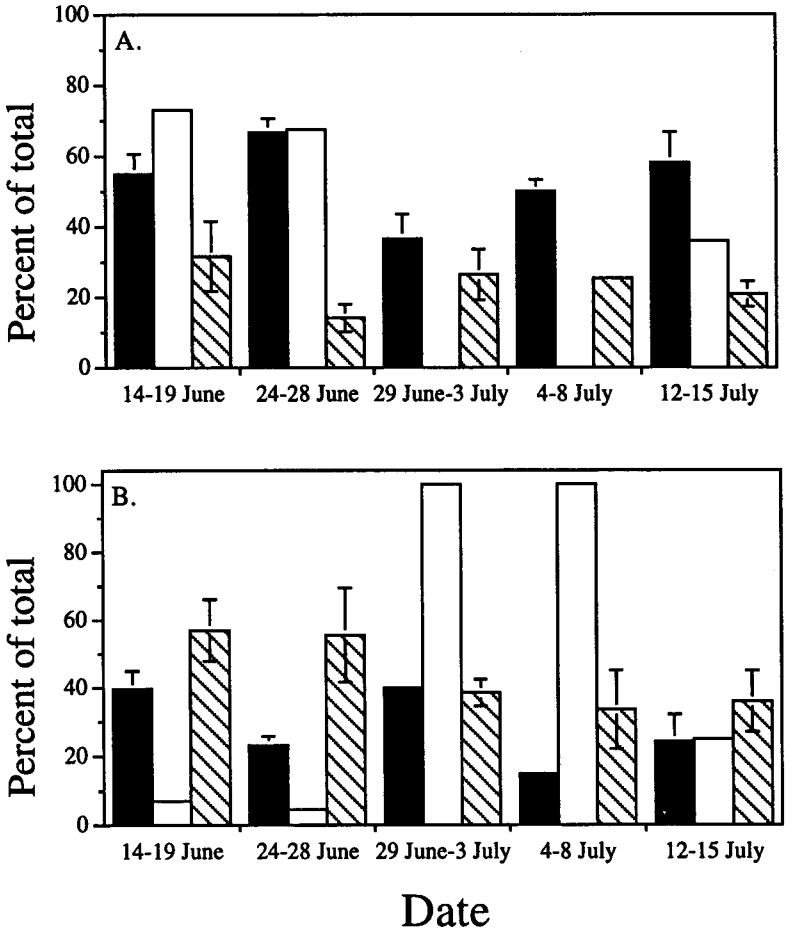

FIGURE 3. Comparison of the percentage of (A) dwarf herrings and (B) sardines delivered by adult Roseate (solid bars) and Sandwich (stippled bars) Terns throughout the chick-rearing period in 1993 with the percent of each species caught by cast net in Turrumote lagoon (open bars) during the same time intervals. Bars represent mean percentage during the 5-day interval, and whiskers represent standard error.

versides were rarely caught by net at Turrumote lagoon during the terns' breeding season, and these fish apparently are absent from coastal waters of Puerto Rico and the Virgin Islands in October and November (Beets and LaPlace 1991, Kimmel 1991). However, during frequent trips to Parguera, I commonly saw them schooling around docks and pilings in coastal areas (ca. 3 km from breeding colonies) from May to July. Thus, Sandwich Terns probably could find sufficient food for their chicks closer to the breeding colonies, and observations of foraging flocks support this belief (Shealer 1996).

Roseate Terns fed chicks primarily dwarf herrings and sardines. This reliance on only a few fish species agrees with other published studies of prey delivered to Roseate Tern chicks in temperate latitudes. In the northeastern United States, sandlance (*Ammodytes* spp.) comprises the majority of the prey fed to chicks, both before fledging (Richards and Schew 1989, Safina et al. 1990) and during the postbreeding period prior to migration (Shealer and Kress 1994). In South Africa, the ratfish (*Gonorhynchus gonorhynchus*) was the most common prey item delivered to Roseate Tern chicks and found scattered around nests, with all other species much less common (Randall and Randall 1978). Diet specialization in Roseate Terns is believed to be a consequence of foraging habitat specialization in this species. Roseate Terns appear to forage selectively over physical (Safina 1990) or biotic

(Shealer 1996) features of the ocean that force prey fish to the surface.

Data on prey diversity and species richness are similar between Puerto Rico and other parts of the world for Roseate Terns. Between 1991 and 1993, Roseate Terns in Puerto Rico fed chicks an average of 7.7 prey taxa per year, similar to Duffy's (1986) report of an average of 6.8 prey taxa per year in a New York colony, based on five years of study. Safina et al. (1990) found that the prey diversity index for Roseate Terns feeding chicks was 1.81, with 73% of all prey deliveries comprised of one species of fish. The diversity index of prey items delivered to chicks at a colony in Connecticut in 1984 was 2.70 (calculated from Table 1 of Richards and Schew 1989). Data from Roseate Tern colonies in other parts of the world are scant, but one study conducted in South Africa presented data sufficient to calculate an index of prey diversity (Randall and Randall 1978) which was 2.71. In Puerto Rico, the mean (± SE) annual prey diversity index was 2.32 ± 0.40 for the three years of study, with a high of 3.08 recorded in 1993. All of the above indices (with minor exceptions where the taxonomy is confused) are based upon prey items identified to species and so are directly comparable. As such, although yearly and colony-site differences exist, the diversity of prey items Roseate Terns feed to chicks does not seem to differ substantially between temperate and tropical colonies.

Diet diversity of adult Sandwich Terns was not statistically greater than that of Roseate Terns prior to chick hatching (3.19 vs. 2.80). However, after chick hatching, daily indices of prey fed to chicks revealed a higher diversity for Sandwich Terns compared to Roseate Terns (4.55 vs. 3.07). Analysis of individual boluses regurgitated by Sandwich Terns in 1993 were different enough to suggest that prior to chick hatching, individual Sandwich Terns fed in different locations. Support for this suggestion comes from the positive correlation between the number of bolus samples on a given day and the combined diversity index, and from observations around breeding colonies in Puerto Rico of Sandwich Terns feeding solitarily around reefs. Unlike Roseate Terns, Sandwich Terns rarely form large flocks over predatory fish schools (Shealer 1996), and so individuals probably encounter different prey patches that contain different species.

The only other published studies of food delivered to Sandwich Tern chicks are those of Pearson (1968) and Veen (1977) conducted at temperate-zone colonies in England. From 1961 to 1963, Pearson found that the diversity of prey delivered to Sandwich Tern chicks was low (calculated index of 2.32 from prey identified to family). Sandlance comprised 74% of all prey deliveries, and clupeids were the second most numerous at only 15%. Veen (1977) also found that the diversity of prey items fed to chicks was low, ranging from 1.88 to 2.52 between 1966 and 1968. Veen argued that Sandwich Terns were highly specialized in prey selection and that this selection was mediated by the chicks themselves, as they often refused fish of species other than sandeels and herring (*Clupea harengus*). Although only two species of fish (dwarf herring and sardine) comprised the majority of chick diets in Puerto Rico, adults also fed chicks a variety of other items including open water schooling fish and reef fish. I found no indication that chicks rejected the less common prey items. Like Roseate Terns, Sandwich Terns in tropical Puerto Rico fed chicks a similar or higher diversity of prey than were fed to chicks in temperate colonies in Europe.

In this study, prey delivered to chicks appeared to be more diverse than prey eaten by adult Roseate Terns, and possibly Sandwich Terns. However, the relationship between prey diversity and breeding performance is not well understood. A diverse prey base was advantageous to Rhinoceros Auklets (*Cerorhinca monocerata*) in the Pacific northwest, which were able to switch from a primary to secondary prey resource following a year of poor recruitment in the primary prey (Vermeer 1980). Tufted Puffins (*Lunda cirrhata*), which nest with Rhinoceros Auklets, apparently were unable to switch to the secondary prey resource, a factor that may have contributed to almost total reproductive failure in that year (Vermeer et al. 1979, Vermeer 1980).

In 1992, the diversity of prey fed to Roseate Tern chicks in Puerto Rico was extremely low at 1.74. In 1992, both Roseate and Sandwich Terns relied much more heavily on dwarf herrings and less heavily on sardines (Fig. 1), suggesting that sardines were less available around the local area than in 1991 or 1993. Roseate Terns in 1992 experienced a dismal breeding season: 23% fewer birds attempted to breed

compared to 1991, mean clutch size was the lowest ever recorded for this population, and reproductive success averaged only 0.26 chicks/pair (Shealer 1995). Sandwich Terns in 1992 were not as drastically affected by the apparent reduction in sardines. They delivered to chicks a higher diversity of prey in 1992 than in 1991, and also experienced moderate reproductive success (Shealer 1995). These findings suggest that Sandwich Terns were able to adjust to a depletion in their preferred prey but that Roseate Terns were less able to use alternative prey resources. Roseate Terns in Puerto Rico are patch specialists and thus presumably sensitive to changes in food, whereas Sandwich Terns feed in smaller, more dispersed flocks and are less reliant on large patches (Shealer 1996).

Primary productivity in tropical marine ecosystems is considered to be low and seasonally invariable compared to temperate latitudes (Raymont 1980). Around Puerto Rico, there appears to be little seasonality in the commercial landings of baitfishes (Kimmel 1991). However, temporal variation exists in abundance and species composition in Turrumote lagoon during the terns' breeding season (Shealer 1995; this study), suggesting that seasonal measures of abundance are scale-dependent. The fish caught by net at Turrumote lagoon probably were not representative of the prey base adult terns delivered to chicks because terns foraged in other habitats, such as the open sea (Shealer 1996), that I was unable to sample.

At a somewhat larger scale, there are pockets of high primary productivity in the Caribbean Sea that are caused by localized regions of upwelling (Kondrat'eva and Sosa 1966, Rossov and Santana 1966). Dinoflagellate blooms occur in the shallow coastal waters of southwestern Puerto Rico adjacent to the tern colonies, and productivity is as much as nine times greater there than in nearby offshore waters (Burkholder et al. 1967). Thus, this area is one region of the Caribbean that experiences high primary productivity and may help to explain the consistent use of the cayos of La Parguera for breeding by terns.

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